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Abstract

Mounting evidence indicates that spatial interactions are important in structuring coastal ecosystems. Until recently, however, most of this work has been focused on seemingly exceptional systems that are characterized by regular, self-organized patterns. In this review, we document that interactions that operate at long distances, beyond the direct neighborhood of individual organisms, are more common and have much more far-reaching implications for coastal ecosystems than was previously realized. We review studies from a variety of ecosystem types—including cobble beaches, mussel beds, coral reefs, seagrass meadows, and mangrove forests—that reveal a startling interplay of positive and negative interactions between habitats across distances of up to a kilometer. In addition to classical feeding relations, alterations of physical conditions constitute an important part of these long-distance interactions. This entanglement of habitats has crucial implications for how humans manage coastal ecosystems, and evaluations of anthropogenic impact should explicitly address long-distance and system-wide effects before we deem these human activities to be causing little harm.

INTRODUCTION

What determines the spatial distribution of species in coastal ecosystems? This question has intrigued ecologists for centuries. The classic perspective on species distribution emphasized the local physical conditions set by the landscape as the main determining factor (Bertness et al. 2014; Lewis 1955, 1964). Typical examples of this viewpoint were exemplified by the theory of zonation, which was developed to account for the zonation of rocky intertidal communities and of salt marsh vegetation. Specifically, early observational research explained distinct bands of sessile invertebrates and macrophytes, which occurred at distinct elevation zones, in terms of physical gradients in inundation duration, heat stress, desiccation, wave action, and other physical stress factors; the optimal position of each species was then explained by its unique capacity to deal with a particular combination of stress factors.

Studies in the 1950s and 1960s expanded this theory by demonstrating that biotic forces are also important in setting species range limits in zonation. For example, some of the earliest ecological experiments demonstrated that the upper distributions of limpets, barnacles, and mussels are set by physiological stress, whereas the lower limits are set by biotic interactions, specifically predation (Paine 1966) and competition (Connell 1961). As a consequence, species were viewed as sorting across predetermined physical landscape gradients, with stress-tolerant species in the harsher upper intertidal areas and less stress-tolerant but competitively dominant and marine-predator-resistant species dominating the more benign lower intertidal areas (Lubchenco 1978, Schiel & Foster 1986). The main premise of this now classic view of the vertical zonation of species in coastal ecosystems is that the interplay between local conditions and local biotic interactions is the main determinant of where species can persist.

Some of the earliest acknowledgments of long-distance interactions in coastal ecosystems originated in research performed in the 1970s, 1980s, and 1990s. Scientists observed that, in some ecosystems, the growth, density, ranges, and persistence of organisms were mediated by long-distance, cross-ecosystem interactions between species living in different, distant environments (Polis & Hurd 1995). Early examples were related to trophic subsidies between adjacent ecosystems (Polis et al. 1997); for example, salt marshes were shown to export significant quantities of plant-derived nutrients (i.e., detritus) to nearby oyster reefs and mudflats and thereby spatially subsidize growth and production in those adjacent but nonoverlapping ecosystems (Odum & Heald 1975). Similarly, spatial subsidies can occur through the displacement of dead material, such as beached whales that drive protein-starved shore communities, or marine snow—the continuous shower of planktonic detritus that fuels deep-sea benthic communities (Polis et al. 1997).

These observations eventually inspired the formulation of the meta-ecosystem concept (Loreau et al. 2003). Long-distance interactions can not only subsidize but also reduce nutrient input in nearby ecosystems. For example, coastal forests bordering estuaries were found to significantly decrease the quantities of freshwater and nitrogen reaching nearby marsh communities (Bertness et al. 2002, Silliman & Bertness 2002). Long-distance linkage can also occur through the passive dispersal (by sea currents) or active exchange (through seasonal migration) of organisms (Polis & Hurd 1995). For example, complex life cycles, such as those of marine bivalves that have a mobile larval phase (transported by currents) and a sessile adult phase, can cause spatial interactions between pelagic and coastal marine habitats in which sea currents that transport larvae determine intertidal population and community dynamics (Gaines & Roughgarden 1985).

A recent example of the effects of active dispersal took place in the Kattegat, located in the eastern Atlantic between Sweden and Denmark. A fishery-induced collapse of the offshore cod stock likely had a strong impact on the inshore seagrass meadows in shallow bays along the Swedish coast, reducing the seagrass cover by up to 40% (Baden et al. 2012, Eriksson et al. 2011,

Moksnes et al. 2008). The cod had used these meadows as breeding and nursery grounds, and their decline triggered a trophic cascade along the coast that increased the abundance of their prey (meso-predators, including wrasses, gobiids, sticklebacks, and common shore crabs). These species functionally removed meso-grazers from the coastal food web and thereby promoted an excessive growth of epiphytic algae that in turn overgrew the seagrass beds, ultimately contributing to blooms of filamentous algae (Eriksson et al. 2009, 2011; Ljunggren et al. 2010). These studies revealed that long-distance interactions can link disjoined ecosystems, affecting local community structures and ecosystem functioning.

In the past decade, a significant body of research has indicated that long-distance interactions are much more prevalent in ecological systems than was previously thought (Rietkerk & van de Koppel 2008). Moreover, these interactions not only occur across the boundaries of specific habitats or ecosystems, but also form an intricate part of the fabrics of ecosystems at different scales and contribute to their resilience (van de Koppel et al. 2005a). One of the most significant general findings from this research is that these interactions often determine rather than follow the spatial organization of ecosystems. Hence, this organization does not passively result from the niche differentiation of species along externally driven environmental gradients, but rather arises from spatial interactions between species. These long-distance, deterministic interactions are most evident in ecosystems that exhibit self-organized spatial patterns, where the interplay of local positive and long-range negative feedbacks between organisms yields regularly spaced spots, gaps, or bands.

The first clear-cut example of spatial self-organization involving long-distance interactions came from arid bushlands, where patches of shrubs and trees form regularly spaced spots or labyrinth-shaped patterns on flat soil and banded patterns on hill slopes. These patterns result from vegetation enhancing water infiltration rates at short distances (1–10 m) and woody species competing for flowing surface water at longer distances (>10 m) (Klausmeier 1999, Rietkerk et al. 2002). Therefore, although the intermediate zones host some annual plants during the wet season, these zones are mostly bare during the dry season.

Further studies revealed that self-organized patterns occur not only in terrestrial ecosystems but also in marine ecosystems. Barnacles can form patterns at very small scales owing to spatially differential competition and facilitation (Bertness et al. 1998). Spatial patterns in seagrass beds arise from scale-dependent interactions between the seagrasses and wave action (van der Heide et al. 2010). Scale-dependent interactions can even generate multiple, nested spatial patterns at different scales within the same ecosystem (Liu 2013). In mussel beds, at the smallest scale (5–10 cm), string patterns arise from individual movement processes, and at a larger scale (5–10 m), regular, banded spatial patterns arise from the interplay of local facilitation between mussels and long-distance competition for algae. In all of these ecosystems, patterns are not imposed by existing landscape gradients but rather result from interacting local and longer-distance interactions between the organisms themselves, generating a self-organizing fabric that determines the spatial shape of the ecosystem.

In this article, we review studies highlighting long-distance biological interactions that shape the spatial structure of coastal ecosystems. Our review reveals that long-distance interactions—interactions that operate beyond the direct neighborhood of individual organisms, ranging from a single meter to many hundreds of meters—are more common and have more far-reaching implications than was previously thought. Examples originating from coastal systems such as cobble beaches, mussel beds on intertidal flats, seagrass beds, oyster reefs, and coral reefs reveal that particular species or communities have cross-habitat or cross-ecosystem effects on others at distances extending beyond the 100-m scale. These examples reveal that, even in ecosystems that do not exhibit conspicuous spatial patterns, long-distance interactions can play a dominant role in creating biogenic heterogeneity at large spatial scales. This has important implications

for how we both use and manage these ecosystems, which we discuss in the last part of the article.

LONG-DISTANCE INTERACTIONS SHAPING COMMUNITY PATTERNS

Cordgrass and Forbs on Cobble Beaches and in Salt Marshes

Plant communities on cobble beaches have proven to be a useful system for studying the effects of long-distance interactions on spatial community structure. Persistent wave action on the beaches combined with the instability of the cobble substrate typically limits the emergence of halophytic beach plants. Yet an upper zone of wave-vulnerable forbs is often present behind lower beds of cordgrass (*Spartina alterniflora*) that absorb wave energy (Bruno 2000). Experiments have revealed that this vertical zonation pattern is the product of scale-dependent interactions, including competition between the cordgrass and the forbs at short distances on the one hand and longer-distance facilitation on the other (van de Koppel et al. 2006) (**Figure 1**). It was found that the baffling of waves by cordgrass facilitated forb growth behind the cordgrass beds while competition for light suppressed forb growth within the cordgrass beds; mowing of vegetation at the upper edge of the cordgrass stands led to the immediate emergence of forb species. Strikingly, cobble beach and salt marsh plant communities, which had previously been studied as separate ecosystem types but which segregate alongshore in gradients of wave exposure and inundation duration, have the same constituent species (van Wesenbeeck et al. 2007). This suggests that scale-dependent interactions are similarly important in the larger-scale zonation of marshes. In both cobble beaches and salt marshes, cordgrass facilitates the growth and survival of plants in the upper intertidal areas through a variety of mechanisms, with the primary differences between these habitats being driven by competitive interactions among plant species (van Wesenbeeck et al. 2007).

Within salt marshes, cordgrass also has important long-distance effects that structure community spatial patterns and dynamics. Cordgrass modifies water flow and increases the deposition of sediments and the accumulation of peat substrate (Redfield 1972). Through this building process and scale-dependent interactions between vegetation growth, substrate building, and water flow, the developing marsh vegetation can generate hummocks (Bouma et al. 2007, 2009; van de Koppel & Crain 2006), elevation gradients, and other landscape features (van de Koppel et al. 2005b), which contrasts with the previous assumption that vegetation zonation is simply a product of elevation gradients (and associated local variations in abiotic and biotic drivers). Over time, however, this process can lead to the marsh being overbuilt—for example, facilitative interactions can stimulate local sediment buildup, increasing the height of the marsh. This overbuilding leaves marshes vulnerable to disturbances that remove the vegetation at the edge, especially when the sediment accumulation becomes so large that the roots no longer stabilize the full developing profile, which can trigger erosional processes and vegetation collapse (Silliman et al. 2012, van de Koppel et al. 2005b). Scale-dependent interactions that reach beyond the patch of marsh grass can also mediate irregular vegetation boundaries (van Wesenbeeck et al. 2008). A perspective that incorporates scale-dependent interactions makes it evident that coastal vegetation can influence ecosystem structure and function beyond its own borders.

Mussel Beds Shaping Tidal Flats

Recent evidence suggests that the zonation of biological communities on tidal flats can be mediated by long-distance, cross-habitat interactions similar to those observed on cobble beaches (Donadi

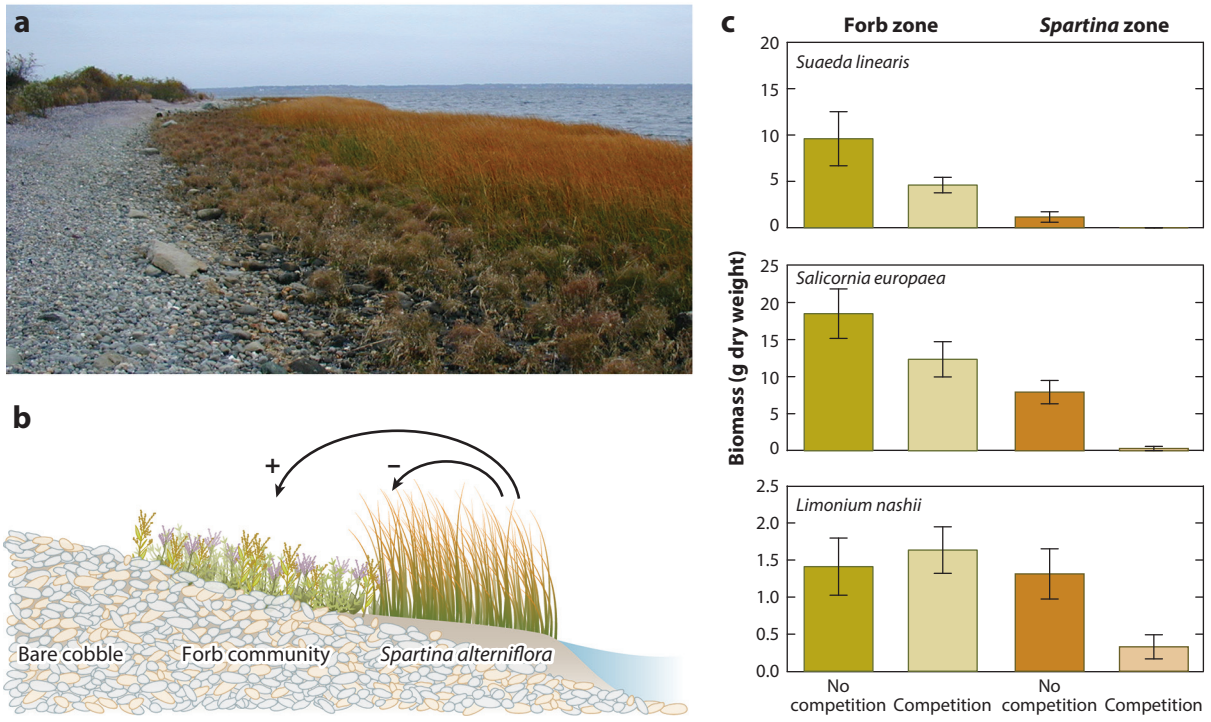


Figure 1

(*a*) Zonation on a cobble beach at Narragansett Bay, Rhode Island, United States. The red band on the right is a fringe of *Spartina alterniflora* that sits on the cobble beach at the water's edge. Between the *S. alterniflora* and the bare cobbles is a zone of forbs that consists mainly of *Suaeda linearis*, *Salicornia europaea*, and *Limonium nashii*. (*b*) Cross section of a cobble beach, showing the zonation of *S. alterniflora* and the forb community. The arrows indicate the edges of a long-distance (± 5 m) effect of the *S. alterniflora* on the forbs, protecting them against waves. (*c*) Results of a transplantation experiment in which juvenile forb plants were transplanted into an *S. alterniflora* zone and into their own zone; each of these two zones was then subdivided into areas with or without competition from neighboring plants. The results revealed the effects of competition, zones, and their interaction, which were significant in all but *Limonium nashii*, where the effect of competition was not significant. Photograph in panel *a* by Johan van de Koppel; panel *b* adapted from van de Koppel et al. (2006).

et al. 2013a, van der Zee et al. 2012). Mussel beds on mudflats reduce current velocities through their physical structure and thereby decrease environmental forcing by tidal energy (Widdows & Brinsley 2002, Widdows et al. 2002, Willows et al. 1998). The reefs also filter large amounts of water, thereby depleting concentrations of algae (Asmus & Asmus 1991, Asmus et al. 1992, Donadi et al. 2013a), which serve as important resources to many other benthic species. In the process of filtering the water, mussels produce organic material in the form of feces and pseudofeces that are deposited on the nearby tidal flat (Bergfeld 1999, Graf & Rosenberg 1997). This deposition results in a complexly patterned mussel bed that consists of multiple habitats with different living conditions and niches with strong variation in grain sizes and pore water chemistry, including silt- and clay-rich habitats (hereafter referred to as muddy habitats) that are characteristic of both oyster and blue mussel reefs. Muddy habitats are not confined to the reefs themselves but often extend both coastward and seaward across the tidal flat in a wide plume; where sediment grain becomes finer toward the reefs, the silt content increases (Donadi et al. 2013a,b; van der Zee et al. 2012).

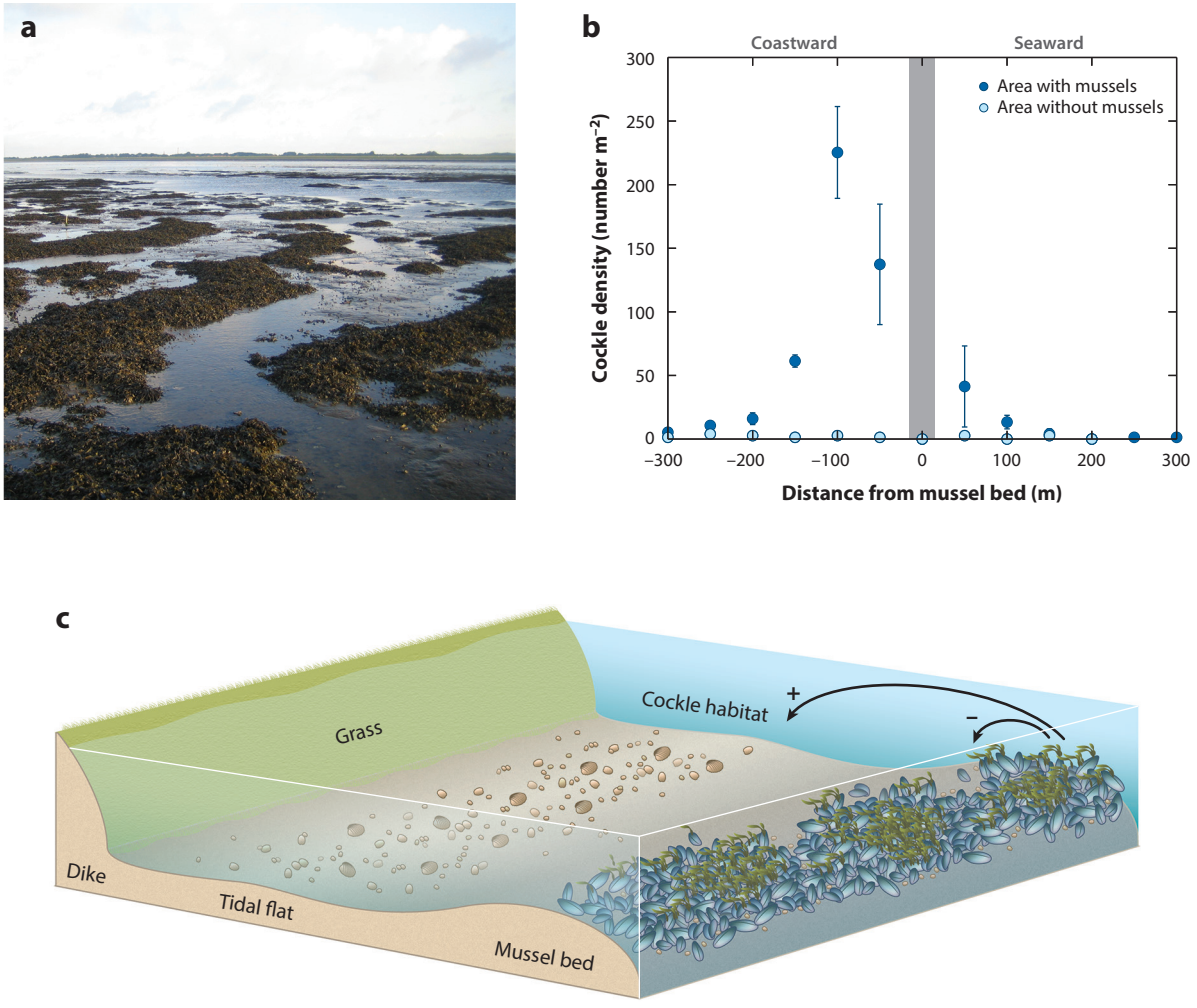


Figure 2

(*a*) A mussel bed near Schiermonnikoog, the Netherlands, at the back of a tidal flat with high densities of cockles living within the sediment. Note that the mussels are covered by macroalgae across a large area of the bed. (*b*) Cockle densities at different points along transects perpendicular to the coast across an intertidal mussel bed (*solid circles*) compared with those in an area without mussels (*open circles*) near Schiermonnikoog, the Netherlands. The gray area indicates the position of the mussel bed. Data are presented as mean ± standard error. (*c*) A cross section through a coast-bound tidal flat. The arrows indicate the facilitative influence on the cockles inhabiting the tidal flat behind and to a small extent in front of the mussel bed. Photograph in panel *a* by Johan van de Koppel; panel *b* adapted from Donadi et al. (2013a).

The physical changes in sediment conditions induced by the mussel beds are reflected in changes in biological communities across trophic levels (Donadi et al. 2013a, van der Zee et al. 2012) (**Figure 2**). Notably, the contrasting effects of mussel beds on the growth and survival of cockles (*Cerastoderma edule*) generate a conspicuous peak in cockle abundances at distances of up to 350 m leeward of the reefs (Donadi et al. 2013a). Experiments have suggested that such increases in cockle abundances are due to the baffling effects that mussel beds have on wave disturbance in the wake of the bed, which facilitates the survival of juvenile cockles (Donadi et al. 2013a).

Accordingly, coastward of mussel beds, exposure to currents and sediment erosion is reduced, and the microphytobenthos, which is limited mainly by sediment erosion on tidal flats, increases strongly both on and in the muddy plume around the mussel beds (Donadi et al. 2013b). However, the mussel beds also deplete food availability in the water and cause degenerated sediment conditions through the deposition of organic material. Thus, within the beds, cockle numbers are highly suppressed, and the low food availability and poor sediment conditions close to the mussel beds substantially reduce their growth (Donadi et al. 2013a). This in turn generates complex alterations to both environmental conditions and organic resources: Coastward of mussel beds, Donadi et al. (2013a) detected reduced exposure to currents and sediment erosion, favoring cockle persistence, but also depleted food availability in the water and degenerated sediment conditions, with increased organic content and decreased oxygen availability.

The microphytobenthos is limited by both sediment erosion and nutrient availability on tidal flats, and primary production therefore increases dramatically both on and in the muddy plume around mussel beds (Donadi et al. 2013a). Yet within the bed, cockle numbers are highly suppressed, possibly owing to competition with the mussels and to the high organic content of the muddy habitats created by the mussels, which leads to potentially toxic conditions for sediment-living bivalves. The low food availability and poor sediment conditions close to the mussel beds create an optimal density of cockles at a distance from the reefs where the impaired growth is balanced against both an enhanced spatfall and an increased survival level for adults caused by the reduced sediment erosion. Hence, similar to the patterns on cobble beaches, the interactions between cockles and mussels are shaped by a scale-dependent interaction: At short distances, resource competition and sediment toxicity dominate, but at longer distances, facilitative interactions prevail. As a consequence, the impact of mussel beds does not stop at the edge of the mussel bed but rather acts at a much larger scale, influencing the tidal flat at distances of up to hundreds of meters from the bed.

The long-distance effects of mussels on the surrounding environment are not limited to a single trophic level; they extend to higher trophic levels as well (van der Zee et al. 2012). Avian species such as oystercatchers (*Haematopus ostralegus*), Eurasian curlews (*Numenius arquata*), and bar-tailed godwits (*Limosa lapponica*) predominantly forage in the wake of mussel beds during low tide, tracking the peak in cockle abundance (van der Zee et al. 2012). This highlights that the interplay of local and long-distance interactions is a strong structuring element in intertidal communities and their associated food webs. This interplay not only leads to the spatial self-organization of mussel beds, as evidenced by the formation of regular patterns, but also structures benthic communities surrounding the mussel beds for distances of up to hundreds of meters and affects the spatial distribution of multiple avian predator species in the area. Hence, the long-distance effects of mussel beds generate self-organization processes that affect entire tidal flat ecosystems.

Oyster Reefs

Oysters can be the dominant reef-forming organisms in temperate and subtropical estuaries, creating mounding structures in deeper water, expansive reefs on large flats, and fringing structures at the water's edge (**Figure 3**). They can have important long-distance ecosystem engineering effects on other components of an ecosystem, primarily through three mechanisms.

First, the physical structure of oyster reefs can affect water flow and attenuate wave propagation. For example, deeper, subtidal reefs modulate water flow, which can modify the flux of food and oxygen to suspension feeders and the deposition patterns of sediment and organic matter (Lenihan 1999). The structure of intertidal oyster reefs can form a barrier in front of marshes that

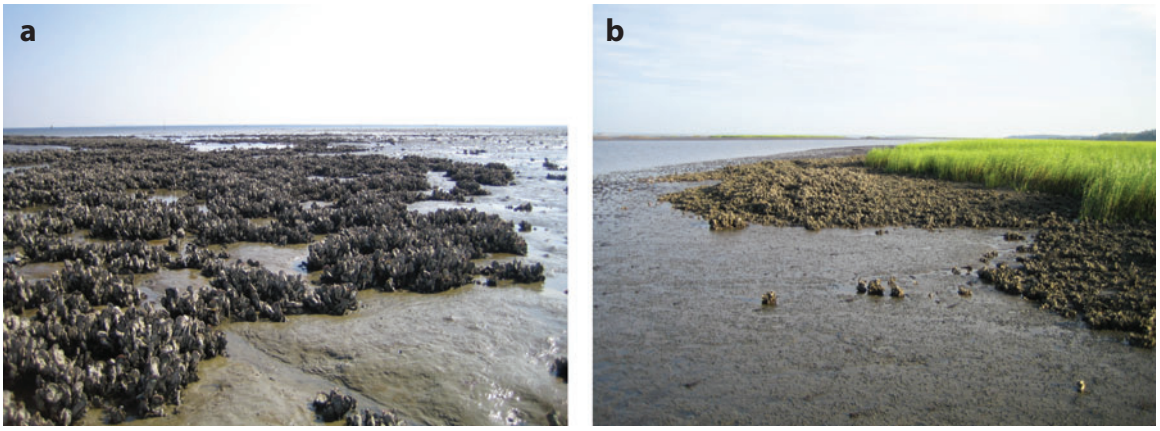


Figure 3

(*a*) An oyster bed in the Oosterschelde, the Netherlands, bounding a tidal flat. (*b*) An oyster bed fringing a salt marsh on Sapelo Island, Georgia, United States. Photographs by Johan van de Koppel.

reduces wave energy, thereby converting erosional conditions into accreting conditions that allow increases in both the size and elevation of the marshes behind oyster reefs (Meyer et al. 1997) (see **Figure 3*b***).

Second, oysters affect water clarity through their filter feeding by removing phytoplankton and sediment from the water column. This in turn affects light transmission and the growth of nearby beds of seagrass and macroalgae, as suggested in modeling (Newell & Koch 2004, Ulanowicz & Tuttle 1992) and mesocosm studies (Wall et al. 2008). Feeding activities of oysters can also affect organisms in downstream habitats by affecting nutrient cycling and availability (Newell et al. 2002).

Third, oysters are connected to other habitats by the movement of mobile organisms that migrate for feeding opportunities (Micheli & Peterson 1999) or to flee periodically stressful conditions (Lenihan et al. 2001). These interactions of oysters can occur at different spatial scales because oyster reefs occur in a variety of configurations in relation to mudflats, seagrasses, and macroalgae.

The value of long-distance engineering by oysters has come to be appreciated only after the widespread decline of oysters caused by systematic overexploitation (Kirby 2004, Lotze et al. 2006). Concerns about shoreline erosion and sea level rise (which translate into property loss) have inspired studies of oyster restoration as an alternative to artificial shoreline hardening (Beck et al. 2011). Oysters can stabilize the shoreline and promote sediment accretion inshore of reefs (as discussed above), with the added benefit that, through feedbacks associated with recruitment, growth, and shell accumulation, oyster reefs can grow and shift to compensate for sea level rise (Grabowski et al. 2012). Hence, these studies show that long-distance, cross-habitat interactions can be harnessed to improve coastal engineering and human safety.

Mussel Beds Interacting with Seagrass Meadows

Subtidal mussel beds and seagrass meadows are often found near each other, in patterns ranging from bands to alternating patches to mixtures. Their very different trophic positions create an opportunity for long-distance, cross-habitat interactions. Similar to the beneficial effects they have on the microphytobenthos, the pseudofeces of mussels act as a fertilizer for nearby seagrass stands, as was shown in both the Baltic Sea and the Gulf of Mexico (Reusch et al. 1994). These

Figure 4

(*a*) Tall *Spartina alterniflora* stands at the edges of a salt marsh on Sapelo Island, Georgia, United States. The tall fringe vegetation blocks access to the inner marsh for the blue crab (*Callinectes sapidus*), one of the main predators of the marsh periwinkle (*Littoraria irrorata*), generating predator release and intense grazing in the inner marsh. (*b*) This blue crab did manage to get a snail. Photographs by Brian Silliman.

potentially positive effects have been experimentally confirmed in mesocosm studies (Wall et al. 2008). However, mussels may also affect seagrasses negatively: The inflow of organic-rich sediment through mussel pseudofeces production can generate anoxic conditions and sulfide toxicity, which may kill the seagrass (Vinther & Holmer 2008, Vinther et al. 2008).

The interactions between mussels and seagrasses are potentially two way. The presence of seagrasses near mussel beds can improve mussel survival, owing to reduced wave action. This strongly suggests that habitats dominated by suspension-feeding bivalves and seagrasses can have facultative cross-habitat mutualistic interactions at the landscape scale (Peterson & Heck 2001). To our knowledge, however, the detailed spatial arrangements of these habitats within a single ecosystem have not been investigated.

Predator Exclusion by Cordgrass Fringes

Marine predators (such as blue crabs and large fish) can strongly suppress the densities of marsh macroinvertebrates where they overlap in space (Silliman & Bertness 2002, Silliman et al. 2004). Both behavioral observations and trapping data indicate that the movement of large predators through the marsh is strongly constrained by vegetation and the tidal cycle (**Figure 4**), such that most predation is concentrated at creek banks (Lewis & Eby 2002, Silliman & Bertness 2002). For example, along the Gulf Coast of the United States, blue crabs are more abundant in marshes with lower platform elevations and at marsh edges owing to obstruction by plant stems (Minello & Webb 1997). Within a given marsh, predation pressure—as demonstrated by tethering and exclusion experiments—is up to an order of magnitude higher at low-elevation platforms compared with higher-elevation platforms (Silliman & Bertness 2002, Stiven & Gardner 1992). As a result, marsh invertebrates, including periwinkles and mussels, are more abundant in the higher-elevation areas, and the powerful effects that these primary consumers generate on the marsh ecosystem structure and function (top-down control of plants, filtration rates, and decomposition) are thus also concentrated in these areas (Hensel & Silliman 2013). Combined, these results suggest that tall cordgrass, confined in distribution to the narrow (1–3 m) creek bank, plays a role in

long-distance interactions that reach into the expansive marsh interior to facilitate marsh invertebrates by mitigating predation pressure.

Long-Distance Reciprocal Facilitation Among Corals, Seagrasses, and Mangroves

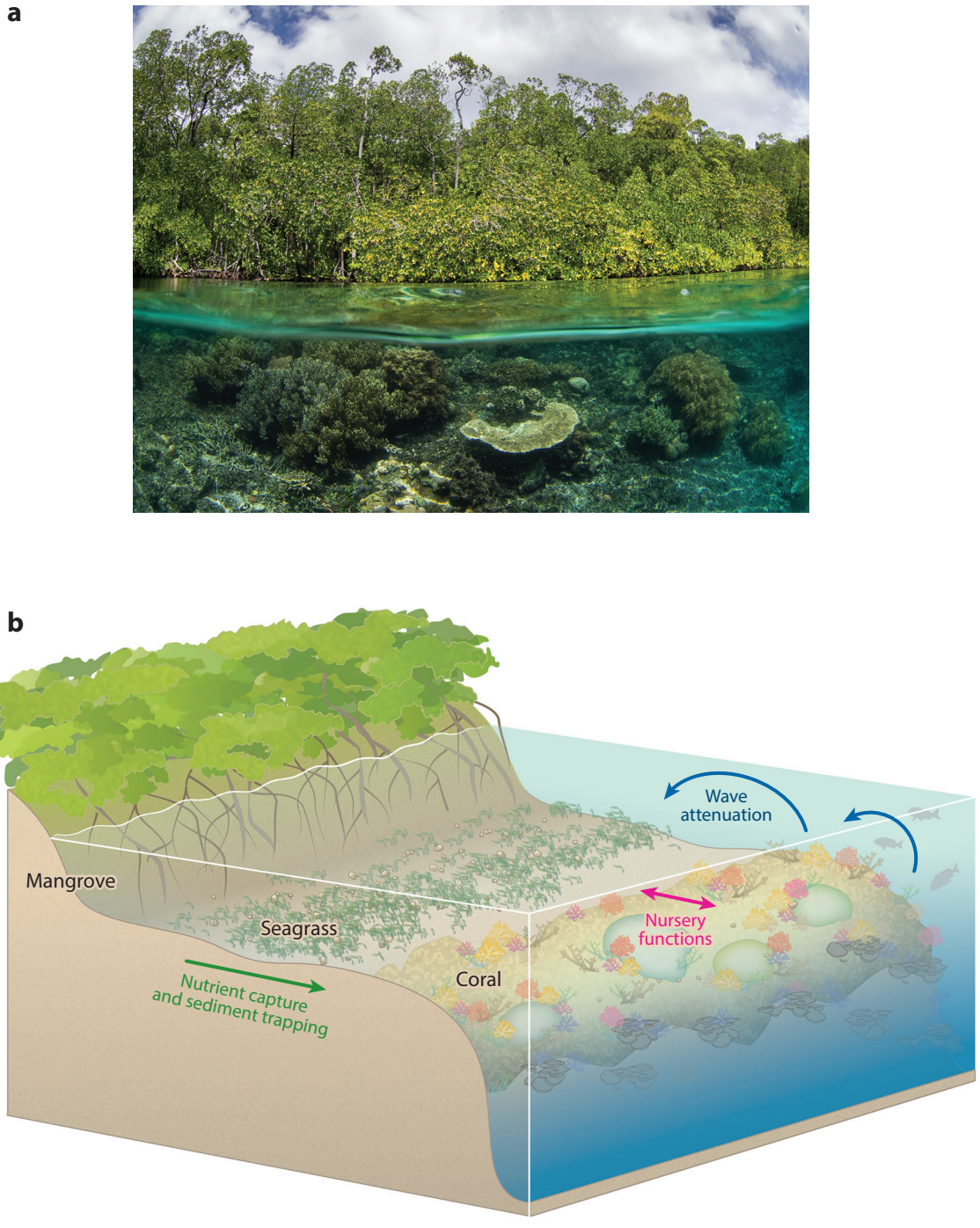
The final, and arguably most spectacular, example of the implications of long-distance, cross-ecosystem effects comes from the interactions between coral reefs, seagrass meadows, and mangrove forests (for a recent review, see Gillis et al. 2014). Coral reefs, seagrass meadows, and mangrove forests form the ecological foundation of many tropical coastal zones. Each of these habitats is among the most productive and biodiverse on the planet and serves as a keystone habitat for thousands of species, including water birds, fish, and turtles. Much of that biodiversity and productivity is supported locally as a result of strong internal positive feedbacks created by the corals, seagrasses, and mangroves. The physical structures of these organisms provide habitats for a large number of species and alleviate abiotic stress (e.g., hydrodynamics, anoxia, and salinity). Moreover, these ecosystems are characterized by highly efficient internal cycling mechanisms—e.g., the stabilization of sediments, trapping of organic particles, and filtering of nutrients from the water layer (Christianen et al. 2013, de Goeij et al. 2013, Hendriks et al. 2010). However, these local feedback mechanisms also form the basis of distinctive long-distance facilitative interactions that all three systems may depend on (**Figure 5**).

A commonly recognized long-distance interaction exerted by coral reefs is the physical protection that they offer to seagrasses and mangroves. Coral reefs are highly resistant to waves, and their complex limestone structure can attenuate wave action. By altering the physical environment, corals engineer not only their own habitat but also any other habitat in their wake, allowing seagrass meadows and mangrove forests to develop in the shallows behind them (Barbier et al. 2011, Moberg & Folke 1999). The corals thereby facilitate a series of other keystone habitats through long-distance interactions (Gillis et al. 2014) that in their spatial extent surpass even the effects of mussel and oyster beds on intertidal communities.

Interestingly, recent research has highlighted that coral reefs, seagrass meadows, and mangrove forests are much more intertwined than is apparent from the one-way protective effects of corals on seagrasses and mangroves. Seagrasses and mangroves provide an important reciprocal service to the corals by trapping sediments and absorbing nutrients (Christianen et al. 2013, Storlazzi et al. 2011). These effects have important implications for corals because they decrease sediment and nutrient fluxes from the hinterland toward the reef. Especially during siltation events, these mechanisms may act as buffers against excess sedimentation, thereby preventing the burial and suffocation of both the seagrass meadows and the coral reefs (Christianen et al. 2013, Rogers 1990, Storlazzi et al. 2011). Because tolerance of high nutrient and sediment loading progressively decreases from mangrove forests to seagrass meadows to coral reefs, a protective cascade forms across these three habitats against algal overgrowth and sediment burial (Gillis et al. 2014). However, the

Figure 5

(*a*) Corals with mangrove vegetation in the background near Yangeffo, Raja Ampat, Indonesia. (*b*) Cross section of a tropical coast with a coral reef at the seaward edge, seagrass meadows in the shallows, and a mangrove forest at the landward edge. The arrows indicate a multitude of reciprocal positive interactions via wave attenuation (*blue*), nutrient capture and sediment trapping (*green*), and nursery functions (*pink*). Photograph in panel *a* copyright © 2013 by Suzy Walker-Toye (**http://www.reefbeasties.com**) and used with permission; panel *b* modified after Gillis et al. (2014) using a schematized layout from US Geol. Surv. (2002).



productivity of the corals themselves is likely also supported by adjacent systems through the import of nutrients, either by the direct efflux of detritus and nutrients (Meyer et al. 1983, Mumby et al. 2004, Nagelkerken 2009) or by the excrement of animals with daily migration patterns, such as turtles that forage on seagrasses during the day but rest on reefs at night (Christianen et al. 2012). Hence, interactions between these shallow coastal habitat types are crucial for understanding the food webs found on top of coral reefs and the productivity and stability of these linked ecosystems on tropical coasts.

Long-distance interactions between the coral, seagrass, and mangrove communities are also created by migrating animals that spend different parts of their life cycles in different habitats. Both seagrass meadows and mangrove forests serve as important nurseries for coral reef fish, thereby enhancing biodiversity (Mumby et al. 2004, Nagelkerken 2009). Indeed, comparisons of areas with and without mangroves suggest that such long-distance interactions may more than double the overall fish biomass on coral reefs (Mumby et al. 2004). Moreover, algivore biomass is typically 30–90% lower on reefs occurring in isolation compared with those that are well connected to both seagrass meadows and mangrove forests (Dorenbosch et al. 2005, 2007; Nagelkerken & van der Velde 2002). This lower number of algivores on isolated reefs enhances the vulnerability of reefs to algal overgrowth (Gillis et al. 2014), which is a main factor associated with reef collapse (Hughes 1994, Knowlton 1992). Additionally, migrating animals may cause indirect long-distance effects. For example, similar to the effects of excrement mentioned above, nutrient fluxes may be affected by animals with daily migration patterns (Christianen et al. 2012).

Our overview emphasizes that the reciprocal, long-distance interactions between coral reefs, seagrass meadows, and mangrove forests form a close-knit interaction network at the landscape scale, linking ecosystems that are often studied in isolation. These long-distance interactions provide benefits to all interacting communities, promoting coral production and protecting seagrass meadows and mangrove forests against waves. Without the combined effects of corals, seagrasses, and mangroves, it is likely that many tropical coastlines would look very different, and the coral-seagrass-mangrove landscape can therefore be viewed as self-organized by long-distance interactions. Although our review is likely biased toward positive, facilitative interactions, and negative interactions are equally likely, the abundance of the examples that have recently emerged in the literature stresses that many marine ecosystems are shaped by a network of consumptive and habitat-modifying long-distance interactions.

TYPES OF LONG-DISTANCE INTERACTIONS

The many examples highlighted above provide a startling view of the importance of long-distance interactions in marine ecosystems. These interactions create unidirectional or even mutual dependence across spatially distinct habitats, similar to what has been found in self-organized ecosystems. The interactions do not create regular patterns, but rather extend or generate new habitats and affect the zonation of species along environmental gradients. On intertidal flats and cobble beaches, such interactions create niches for species that would otherwise not be able to persist there, even though the facilitating species inhabits a spatially different habitat. Hence, even in the absence of regular spatial patterns, the spatial structures of these ecosystems may—in part—be regarded as self-organized, i.e., also resulting from local interactions between species rather than imposed only by the landscape. They are therefore of similar importance for both community composition and ecosystem functioning.

In *On the Origin of Species*, Darwin (1859) provided his early view of how natural communities could be characterized by the interactions between their inhabiting species:

> It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us. (p. 489)

The cross-habitat interactions in coastal ecosystems highlighted in this review create dependencies not only between species living within the same habitat but also between those living in spatially separate habitats, potentially even creating conditions for entirely new habitats that would not exist without such interactions. Hence, beyond what Darwin contemplated, marine ecosystems form an elaborate "spatially entangled bank" that is shaped by both feeding interactions and habitat-modifying interactions operating at extensive spatial scales.

Our review of long-distance interactions in specific marine ecosystems reveals diverse types of between-habitat and between-ecosystem interactions that impact community structure. The first type that we distinguish arises from the effects of consumers that both migrate and impose a high grazing or predation pressure on a specific habitat because they are subsidized by food sources from afar. Because many large predators are often very mobile, this type of interaction is likely to be common. It could also result from consumers entering a habitat as juveniles, as has been found on coral reefs. The second type arises from long-distance competition through depletion by mobile resources, such as the depletion of algae from the water column over a mussel bed, which affects cockle growth in the mussel bed's wake, as observed in the Wadden Sea (Donadi et al. 2013b). A third type could be caused by a supply of nonliving substances moving from one ecosystem to another, in the form of fluxes of nutrients or organic matter, as was found in salt marshes and kelps subsidizing offshore areas (Duggins et al. 1989). Finally, a fourth type could arise when organisms in one habitat or ecosystem affect physical processes such as wave action or water flow and thereby modify the environment that exists in another habitat or ecosystem, as found on cobble beaches (van de Koppel et al. 2006), in mussel and oyster beds (Donadi et al. 2013a), and between tropical ecosystems (Gillis et al. 2014). These interactions can be negative (e.g., inhibiting the growth and survival of organisms in the recipient community) but can also be positive (e.g., facilitating the growth and survival of those organisms).

In this review, we have made a distinction between long-distance interactions that occur within ecosystems and those that occur across ecosystems. An example of a within-ecosystem interaction is the effect that mussel beds have on the tidal flat that surrounds them; an example of an across-ecosystem interaction is the effect that the removal of terrestrial forests has on marine seagrasses. This distinction is artificial and is determined by the timescale under consideration. For instance, mangrove forests reduce erosion and thereby maintain terrestrial habitats, but they also prevent nearshore seagrass beds from becoming a tidal wetland because of excessive sedimentation. This illustrates that when space and time are considered at sufficiently long scales, all interactions occur within the global ecosystem, and long-distance effects are important structuring elements even at global levels (Swap et al. 1992).

IMPLICATIONS FOR THE MANAGEMENT OF ESTUARINE AND COASTAL ECOSYSTEMS

The studies reviewed above have revealed processes that have crucial implications for current paradigms in the management of estuarine and coastal ecosystems. The policies involved in managing these ecosystems often revolve around a central premise: that the effects of human activities such as fisheries and dredging are localized, i.e., restricted to the localities, habitats, and species

that are directly affected by human exploitation and disturbance. As a consequence, management policies can sometimes allow for limited human exploitation of these ecosystems on the assumption that they will only locally impact the exploited populations and will not affect the functioning of these ecosystems at larger spatial scales.

The multitude of studies reviewed above highlights that this assumption may be too restrictive. The existence of long-distance, cross-habitat interactions that reach beyond the habitats of particular species implies that the effects of human disturbance can spatially cascade across ecosystems, affecting other habitats at distances of hundreds of meters—or even farther away, if an affected habitat in turn interacts with another, more distant habitat. For example, the exploitation of mussel beds by fisheries can impact an entire tidal flat, affecting microbial production, benthic production, and avian predators far beyond the confines of the area affected by mussel harvest, a cascade that can affect ecosystems at distances a kilometer or more from human activity. The same principle holds for the other examples reviewed above.

This review is not a plea for the total cessation of human activities, such as benthic fisheries, in estuarine and coastal ecosystems. But it calls for a thorough analysis of spatially cascading effects across habitats and areas with different protection statuses, especially sensitive and important areas where precautionary principles apply. Specifically, we recommend the following important changes in policy doctrines:

- Human activities should be excluded or limited at larger spatial scales than are currently considered. For example, in areas where human activities are restricted in order to preserve intertidal soft-bottom ecosystems, such protections should be implemented across tidal flats or even entire tidal basins rather than only at the scale of specific habitats (e.g., individual mussel beds).
- Longer-distance, cross-habitat interactions should be addressed at all relevant trophic levels. This implies spatial scales of many kilometers, covering the daily movement distances of avian predators and predatory fish.
- Long-term protection should, in particular, be provided for habitats that are dominated by so-called foundation species, such as mussels, oysters, corals, seagrasses, and mangroves, which often exert long-distance effects on surrounding habitats. The habitats of these organisms can take decades to recover from disturbances, and their destruction is often difficult to reverse.

Implementing these proposals will be instrumental in maintaining the long-term stability in these often highly valued marine ecosystems. Moreover, they will facilitate a new approach to ecosystem-based management that extends its consideration of human influence across habitat and ecosystem boundaries.

Importance for Marine Protected Areas

Marine protected areas (MPAs) offer a valuable opportunity to apply the perspective of long-distance interactions because they are by definition part of a spatially explicit conservation and management strategy. One widely recognized benefit of MPAs is the so-called spillover effect—the enhancement of fisheries outside reserve boundaries owing to the emigration of adults or the dispersal of propagules from inside reserves (Gell & Roberts 2003). We suggest that the long-distance interactions of foundation species contribute to such spillover effects not only by providing critical habitats that enhance fishery production, but potentially also by performing ecosystem engineering of the physical environment that extends beyond the reserve boundaries.

For example, coral reefs in an offshore MPA can reduce wave stress on more inland ecosystems, and mangroves in an onshore MPA can protect more seaward ecosystems. In addition, spillover effects may provide additional valuable services to society, such as mangroves protecting inland areas from tsunami and storm damage (Danielsen et al. 2005). The importance of foundation species has already made the presence of such species a main criterion for the placement of MPAs (Leslie et al. 2003), and we argue that the long-distance effects of these species beyond reserve boundaries should also be explicitly considered in MPA design. Increased care should also be taken to prevent spill-in effects, in which the functioning of key habitats in relatively small MPAs depends on unprotected habitats beyond their borders: In-shore habitats such as mangrove forests and salt marshes are frequently not included in MPAs even though they may play an important role in sustaining the reserves. Thus, the importance of cross-scale interactions calls for an ecosystem- and landscape-based approach to conservation.

Several considerations affect how long-distance interactions such as those propagated by foundation species should factor into MPA design. First, there are commonly nonlinear relationships between the sizes of foundation species habitats and the long-distance effects that these species have on habitat modifications (Barbier et al. 2008, Koch et al. 2009). Second, MPAs are unable to protect against some threats, such as oil spills and invasive species that move across reserve boundaries (Allison et al. 1998). Both of these considerations are factors in the many-small versus few-large argument over MPA design owing to diminishing returns on the size of foundation species habitat (Barbier et al. 2008). Third, the design of MPA boundaries should consider how multiple foundation species are interconnected through long-distance interactions mediated by the modification of physical conditions and the movement of organisms and resources (Angelini et al. 2011, Guichard et al. 2004). For example, coral reefs protect seagrasses and mangroves by attenuating wave stress, and seagrasses and mangroves in turn buffer coral reefs from terrestrial sediment and pollution and act as nurseries for fish that later migrate to coral reefs. In such a system, protecting either offshore coral reefs or inshore seagrass and mangrove habitats alone would be insufficient to maintain ecosystem function.

Importance for Coastal Protection Against Sea Level Rise and Storms

Recent studies have highlighted that long-distance interactions can be important for coastal defense against globally rising seas and increased storm frequencies (Barbier et al. 2008, 2011; Koch et al. 2009; Temmerman et al. 2013). Whereas classical coastal defense strategies focus on a single barrier against high water levels, a new strategy has recently been proposed that integrates the services that many coastal ecosystems provide into what is called an ecosystem-based coastal defense (Gedan et al. 2011, Möller & Spencer 2002, Shepard et al. 2011, Temmerman et al. 2013). This new paradigm harnesses the long-distance effects that coastal communities have on one another and on the main seawall to better protect the seawall against wave damage. For instance, in temperate regions, the seawall may be fringed at the seaside by salt marshes, which in turn are bounded by mussel and oyster beds at the fringes or on the tidal flat in front of the salt marsh. Beyond their direct effect on wave action, mussel and oyster beds may play an important role in stimulating sedimentation both in the tidal flats they inhabit and in the salt marshes, improving growth conditions for vegetation (Eriksson et al. 2010). The vegetation itself is an important factor in attenuating waves before they reach the seawall, not only protecting the seawall from wave damage during storm conditions but also reducing maintenance costs. Hence, the protective properties of coastal ecosystems result from a cascade of long-distance facilitation effects, in which the oysters facilitate the salt marsh and the salt marsh facilitates the seawall.

SUMMARY

In this review, we have presented recent evidence for long-distance interactions and their importance for ecosystem functioning and biodiversity. Although some examples of long-distance interactions stem from older studies, many of them are very recent, suggesting that the presence of long-distance interactions is not immediately evident in many ecosystems. This may be a consequence of the massive global decline of key marine habitats over the past 50 years, which is unfortunately ongoing in many parts of the world. The surface areas of mussel beds, oyster reefs, coral reefs, seagrass meadows, and mangrove forests are strongly decreasing each year (Bellwood et al. 2004, Eriksson et al. 2010, Valiela et al. 2001, Waycott et al. 2009). This implies that the marine ecosystems that we observe today may lack many of the important long-distance interactions that characterized them at times when human exploitation was less intense, and their current state may not be representative of how these systems functioned in the past (Gillis et al. 2014). Hence, beyond locally improving environmental conditions, restoration practices should consider the long-distance interdependence between habitats and ecosystems when aiming to restore or reestablish marine communities.

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Contents

Errata

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